THE ZINGIBERALES (CANNACEAE, MARANTACEAE, AND ZINGIBERACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

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The order Zingiberales (Scitamineae, Scitaminales) is clearly delimited and is universally accepted as a natural group of four to eight families, depending on the ranks assigned to some of its chief components. Emphasizing anatomical evidence in addition to morphology, Tomlinson (1962, 1969) advocated recognition of Zingiberaceae, Costaceae (often included in Zingiberaceae), Marantaceae, Cannaceae, Musaceae, Lowiaceae, Heliconiaceae, and Strelitziaceae (the last three often included in Musaceae). Other recent authors differ as to which of the segregates are chosen for elevation to the rank of family. Zingiberaceae, Cannaceae, and Marantaceae are represented in the southeastern United States by a small number of indigenous and introduced species.

Transformation of stamens into sterile staminodes is a well-known trend bearing on the interrelationships of the families of Zingiberales. The Musaceae

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and its segregates have five or rarely six fertile stamens, a condition that invites interpretation as primitive (see pertinent discussion in Dahlgren). Zingiberaceae *sensu lato*, Marantaceae, and Cannaceae have only one fertile stamen, with the others developing as petaloid staminodes or sometimes absent; in the two latter families half of the fertile stamen is petallike. Comparison of the families is provided in the key below, where further ties between the Cannaceae and Marantaceae—and characters separating these families along with Zingiberaceae from Musaceae *sensu lato*—are enumerated. Inviting as it may be to extrapolate a phylogenetic scheme from the characters in the key, the cladistic relationships of the eight putative families of the Zingiberales are obscured by contradictory characters, uncertainties surrounding homologies of apparent similarities (e.g., the diverse "arils" and chalazal inclusions in the seeds), and insufficient sampling for several characters. Phylogeny within the order and problems with its assessment were discussed by Tomlinson (1962), who suggested Strelitziaceae as the least specialized family.

The best taxonomic position for the Zingiberales is debatable. Hutchinson derived them from the Bromeliales (one family), and these from Commelinales. Bromeliales and Zingiberales were thought by Takhtajan to have a common origin from lilialean stock; Cronquist (1978, 1981) united the two orders as subclass Zingiberidae. In Thorne's scheme, the Zingiberales were placed in superorder Commeliniflorae along with the Bromeliaceae (a member of the Commelinales). Superorder Zingiberiflorae (containing only the Zingiberales) was hypothesized by Dahlgren (p. 140) to have arisen from liliiflorean ancestors on a "pro-commeliniflorean-zingiberiflorean-bromeliiflorean branch."

A prevalent concern in the literature on Zingiberales is interpretation of their androecia in terms of a presumably ancestral arrangement with three stamens in an antesepalous outer cycle alternating with three others in an antepetalous inner cycle. Interpretations involving patterns of venation, and positional, teratological, developmental, and anatomical evidence bearing on this matter are reviewed in Costerus (1916a, 1916b, 1916c), Eichler (1873; 1884, under Marantaceae), Holttum (1950, under Zingiberaceae), Kirchoff (1983b), Rao *et al.*, and Schachner. A brief overview follows.

In the relatively uncontroversial Marantaceae the inner cycle of the androecium probably includes the fertile stamen with its lateral appendage, the cucullate staminode, and the callose staminode (synonymy for these floral parts is provided with the family description). The outer cycle must then be represented by one (usually) or two petallike staminodes, with the third member suppressed. Support for this widely accepted interpretation appears in developmental studies by Eichler (1884) and Kirchoff (1983b): both observed a primordial ring, positioned above the calyx, which splits tangentially in each of the three alternisepalous positions to yield altogether three petals to the outside and three members of the androecium (fertile stamen, cucullate staminode, and callose staminode) to the inside. Primordia for the remaining (outer) staminodes are antesepalous. Eichler found floral vasculature to corroborate the developmental evidence (see also Tilak & Pai, 1966, 1968).

On the basis of developmental similarities, studies of Eichler (1884) and Kirchoff (1983b) agree further that flowers of Cannaceae are fundamentally as described above for Marantaceae, with one or two (or sometimes no) petallike staminodes representing the outer androecial cycle, and with the labellum, one petallike staminode, and the fertile stamen (or no) as the inner cycle. According to both authors, these structures are homologous with the marantaceous cucullate staminode, callose staminode, and fertile stamen, respectively. Marantaceae and Cannaceae have been said to differ in the sequence of initiation of calyx lobes: those of Cannaceae spiraled in the same direction as the corolla and androecium vs. the spirals opposed in Marantaceae. However, Costerus (1916c) observed in a species of *Canna* many instances in which the calyx and corolla formed opposite spirals.

Few contemporary observers would dispute that in the Zingiberaceae the inner staminal cycle is represented by two staminodes connate to form the labellum plus the separate fertile stamen; clearly the outer cycle is sometimes (e.g., in Hedychieae) manifest as two free petaloid staminodes. However, the fate of the third (median) outer staminode, which is never unambiguously apparent, and the whereabouts of the two lateral staminodes when they are not obvious, remain problematic. Authors commonly consider fusions with the labellum as potentially accounting especially for the recondite median staminode (e.g., see Costerus, 1916b; Gregory), and sometimes for all three outer staminodes. Pai (1965b, 1966), however, stressed vascular evidence, while arguing in favor of the "classical view" that the labellum in at least some Zingiberaceae involves only the two inner staminodes. At the other extreme, the labellum composed of all five staminodes has been numbered among the characters that distinguish *Costus* L. (-oideae, -aceae) (see Costerus, 1916b; Cronquist, 1981; Holttum, 1950; Loesener; Maas, 1972; Schachner; Thompson, a contrary conclusion; Tomlinson, 1956; several of the references in this and the following paragraph are listed under Zingiberaceae). This distinction is best regarded as open to refinement. In some genera of Zingiberoideae, the lateral staminodes are ostensibly manifest as large or small lobes or teeth on the labellum.

Dampening the temptation to regard all lobes on the labellum in Zingiberaceae as adnate outer staminodes, Burtt (1972) pointed out that the elaborately lobed labellum of some orchids is homologous with a single perianth member. He also observed that the number of lobes on the zingiberaceous labellum in some cases exceeds the number of missing staminal components. Moreover, in *Hedychium coronarium,* in which the lateral staminodes are strongly and distinctly developed, the labellum sometimes has lateral lobes.

Contrary to interpretations of the epigynous glands of Zingiberaceae as modified stamens or styles, these nectaries have been shown to be vascularized carpellary outgrowths that range in position from being enclosed within apically open ovarian cavities in Costoideae to rising vertically above the summit of the ovary in Zingiberoideae (Pai, 1966; Rao).

GENERAL DESCRIPTION OF ZINGIBERALES:

Small to arborescent, perennial, rhizomatous, mostly terrestrial herbs typically of moist tropical habitats. Hairs mostly unicellular. Leaves usually petiolate, with sheathing bases (these often forming a pseudostem around a feeble true stem); blade entire, rolled in the bud, with a multistranded midrib region and many pinnate-parallel, lateral nerves; leaf axis usually with septate air canals. Inflorescences often with large, folded to spathelike, colorful primary bracts. Flowers usually perfect, zygomorphic or asymmetric, typically showy. Sepals 3, unlike the petals; petals 3, often unequal. Androecium the showiest portion of the flower (in our families), arranged fundamentally in 2 trimerous cycles; fertile stamen 1 [or 5 or 6], when 1 the flower with showy staminodes, these diverse in number, form, arrangement, and fusions, usually showier than the perianth. Gynoecium 3-carpellate, syncarpous and basically 3-locular (2 locules sometimes aborting), with 1 to many ovules per locule, ovary inferior [or flowers perigynous], style single. Seed with a specialized region of dehiscence, often operculate, usually with a micropylar collar, usually arillate (or with arillike emergences from the funiculus).

KEY TO THE FAMILIES AND GENERA OF ZINGIBERALES IN THE SOUTHEASTERN UNITED STATES[2]

A. Functional stamens 5 [or 6]; raphide-sacs present; guard cells with the inner and outer ledges equal. MUSACEAE (plants often of treelike appearance and size, with lateral buds opposite the leaves in *Musa*). . . . . [*Musa*.[3]]

A. Functional stamen 1; raphide-sacs absent; guard cells with the inner and outer ledges unequal (except in Cannaceae).

B. Leaf sheaths ligulate (FIGURE 1, b); flowers zygomorphic; sepals connate into a tube usually slit along 1 side (FIGURE 1, g); sterile staminodes represented by a usually broad labellum composed of 2 or more fused staminodes (the dual nature not readily evident) flanked by and sometimes adnate to 2 petallike to much reduced (to not detectable) lateral staminodes; anther with 2 locules, the style lying between them (FIGURE 1, h), on a nonpetaloid filament; pollen not deposited onto style in bud; nectaries vascularized emergences of carpellary tissue [or sometimes concealed in cavities]; endosperm development helobial. ZINGIBERACEAE.

C. Lateral staminodes strongly developed and petallike (FIGURE 1, g); labellum more or less flat (not troughlike), white to yellowish or marked with yellow; corolla tube several centimeters long; none of petals hoodlike. . . . . 1. *Hedychium*.

C. Lateral staminodes not apparent or reduced to small teeth; labellum troughlike, yellowish (especially toward the margin) or white, with reddish markings (especially toward the center); corolla tube to ca. 1 cm long; 1 petal hoodlike and facing labellum. . . . . [*Alpinia*.[4]]

B. Leaf sheaths without ligules (sometimes auriculate); flowers asymmetric; sepals distinct; sterile staminodes variously arranged but all distinct (except for basal

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[2] For embryological comparisons of these families, see Panchaksharappa (under Zingiberaceae).

[3] Species of *Musa* L. are sometimes found growing outside of cultivation in Florida (and, according to Small, in Louisiana). Such occurrences appear to result usually, if not always, from persistence after cultivation, from rhizomatous spreading, or from inadvertent distribution by humans. Available evidence does not confirm bananas as truly naturalized components of the flora of the southeastern United States (see Black & Black, Lakela & Craighead, Long & Lakela, Melvill, Poppleton *et al.*, Thieret, Ward, Wunderlin, and acknowledgments in footnote 1).

[4] For comments on *Alpinia* Roxb., nom. cons., in the southeastern United States, see Zingiberaceae.

fusions); anther with 1 locule, the remainder of stamen petaloid or partly so; pollen deposited onto style in bud; nectaries septal; endosperm development nuclear.

D. Petioles not pulvinate at apex; stem with mucilage canals; staminodes consisting of a labellum and [0 or] 2 or 3 petallike staminodes (none of these hoodlike or appendaged) (FIGURE 2, d, e); style more or less petaloid, not curling inward, the region of pollen deposition not specialized, the stigma apical and marginal (FIGURE 2, k); gynoecium 3-locular, with many ovules per locule; seed opening by a slit, without canals in the (mostly chalazal) nutritive tissue; embryo straight; flowers single or in homodromous pairs. CANNACEAE. . . . . 1. *Canna.*

D. Petioles pulvinate at apex; stem without mucilage canals; staminodes consisting of an appendaged, pouchlike "cucullate" staminode (FIGURE 3, g) enclosing the style before pollination, a hoodlike "callose" staminode (FIGURE 3, h), and 1 or 2 petallike staminodes; style not petaloid, curling rapidly inward when dislodged and effecting pollination, with a specialized region of pollen deposition (FIGURE 3, k-13), the stigma in a cleft (FIGURE 3, k-14); gynoecium unilocular (in ours), with 1 ovule per locule; seed operculate, with 1 or 2 canals in the (nucellar) nutritive tissue; embryo bent; flowers in mirror-image (antidromous) pairs (this not always conspicuous in *Maranta*). MARANTACEAE.

E. Petals distinct or nearly so; cucullate staminode with 2 appendages (FIGURE 3, g); outer petaloid staminode 1 (FIGURE 3, f); stigmatic cleft with a bifid rim projecting back into the flower (FIGURE 3, i–k); axes of flower pairs condensed (flowers of a pair borne tightly side by side; FIGURE 3, b); canal in seed forked at the base (in effect 2 canals). . . . . 1. *Thalia.*

E. Petals connate into a tube; cucullate staminode with 1 appendage; outer petaloid staminodes 2; stigmatic cleft more or less funnel shaped; axes of flower pairs elongate; canal in seed forked only at the apex. . . . . 2. *Maranta.*

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ZINGIBERACEAE Lindley, Key Struct. Phys. Syst. Bot. 69. 1835, nom. cons.

(Ginger Family)

Aromatic, small to large herbs with short, distichous-scaly, thickened [or long, thin] rhizomes, these branching sympodially from axils of scale leaves near the bases of erect [or sometimes very short] stems, each branch potentially terminating in an unbranched leafy shoot [branched in some Costoideae] and/or an inflorescence. Hairs unicellular (Zingiberoideae). Plants with aromatic oil cells (Zingiberoideae). Leaves basal or cauline, sometimes petiolate, distichous [spirally arranged in Costoideae]; sheaths overlapping (in Zingiberoideae often forming a pseudostem surrounding or overtopping a thin true stem), open [or closed], adaxially ligulate at insertion of petiole; blade often asymmetric; stomata mostly tetracytic (paracytic to polycytic). Inflorescence(s) terminal [sometimes falsely appearing to be lateral], borne on a leafy shoot [or on a peduncle covered by distichous, bladeless sheaths arising from the rhizome], usually simple [sometimes branched or uniflorous], often with a condensed headlike or conelike appearance, the main axes bearing spirally arranged [or rarely distichous] primary bracts subtending variably modified [sometimes 1-flowered], condensed cincinni, these with variable higher-order bract(eole)s, sometimes with basal 2-keeled prophylls. Flowers perfect [rarely imperfect], highly diverse in appearance, usually lasting only 1 day, mostly zygomorphic. Sepals connate into a tube (sometimes not readily distinguishable as 3 units), the tube usually split along 1 side and lopsided. Petals fused basally with the androecium into a usually narrow tube, the dorsal lobe usually larger than the other lobes [and sometimes appendaged]. Androecium highly modified, variable in appearance, composed of 1 fertile stamen; a usually large, petaloid, often 2-lobed labellum (usually the largest organ of the flower); and sometimes 2 petaloid [to toothlike] lateral staminodes more or less free [or fused to labellum]. Anther with 2 locules [sometimes variably broadened or appendaged]; pollen grains 2-nucleate when shed, usually inaperturate (Zingiberoideae), spinuliferous to more or less psilate. Gynoecium usually with 2 variable "epigynous glands" (nectaries) jutting into the floral tube apically from the ovary (Zingiberoideae); ovary 3-locular with axile placentation [or 1-locular with parietal, basal, or free central placentation, rarely 2-locular]; ovules more or less anatropous, usually numerous; style thin, usually passing through a channel in the filament and between the locules of the anther; stigmas diverse in form, usually ciliate, often sunken. Fruit capsular [or indehiscent, then fleshy or dry, sometimes opening by disintegration of the walls]. Seeds usually arillate, operculum well [to poorly] developed, endosperm development helobial, with perisperm and endosperm (sometimes with variable intrusions of chalazal tissue); embryo straight, cylindrical, or club shaped. Megagametophyte (embryo sac) of the Polygonum type (Zingiberoideae) [Adoxa type reported in *Costus*]; base chromosome numbers variable, including 9, 11, 12. (Including Costaceae Nakai, Jour. Jap. Bot. **17:** 203. 1941; Alpiniaceae Small, Man. Southeast. Fl. 360. 1933.) TYPE GENUS: *Zingiber* Boehmer, nom. cons.

A pantropical (to subtropical) herbaceous family, comprising over 1000 species in some 40–50 genera (over a third of these with very few species), typical of floors of lowland forests. Subfamily Zingiberoideae, encompassing by far the greater part of the family and subdivided into four tribes, is centered in tropical mainland Asia and the Malay Archipelago including Papuasia; only *Renealmia* L. f., nom. cons. (ca. 75 spp.), extends naturally to the New World. (It also occurs in Africa.) Subfamily Costoideae (Meisner) K. Schum. is made up of the pantropical *Costus* (80^+ spp.), the small genera *Dimerocostus* Kuntze and *Monocostus* K. Schum. in tropical America, and *Tapeinochilos* Miq., nom. cons., which ranges from eastern Indonesia to Queensland. No extant species of Zingiberaceae is indigenous to the continental United States.

In Florida *Alpinia Zerumbet* (Pers.) B. L. Burtt & R. M. Sm. (*A. speciosa* (Wendl.) K. Schum.; *Languas speciosa* (Wendl.) J. K. Small), of tribe Alpinieae, persists after (or infrequently escapes from) cultivation, and *A. officinarum* Hance reportedly persists after cultivation (see Lakela & Craighead; Morton, 1976; Poppleton *et al.*; Small; Ward; Wunderlin; and acknowledgments), but neither appears to have become a component of the local flora. In Florida *Hedychium coronarium*, of the tribe Hedychieae, is more widespread outside of cultivation than the species of *Alpinia.*

Zingiberaceae are characterized vegetatively as mostly terrestrial, rhizomatous, sometimes large herbs with aromatic oils in specialized cells (Zingiberoideae) and with ligulate leaf sheaths. Diversity in overall form disguises a basic floral construction that helps to unify the family: the tubular calyx tends to split along one edge; the corolla and androecium form a tube, from which arise three petals, often two petallike to toothlike (or inconspicuous or absent) lateral staminodes, one fertile stamen bearing a complete anther, and a usually large labellum formed by the fusion of at least two staminodes. The thin style characteristically lies in a groove in the filament and passes between the locules of the anther. The arillate seeds contain straight embryos.

Polyploid and aneuploid changes are notable aspects of the evolutionary history of the Zingiberaceae. In fact, according to Sharma & Bhattacharyya, visible changes in chromosome complements have been sufficiently pervasive for different species typically to have different karyotypes. These authors, who studied both wild and cultivated Zingiberaceae, found that chromosomal heterogeneity is significant even within individuals. A second noteworthy cytological aspect of the family is that it should probably be counted along with the Juncaceae, Cyperaceae, and Musaceae(?) as one of the few families containing species that have chromosomes with diffuse centromeres (Grant).

A taxonomic history is available in Holttum's (1950) partial revision of the Zingiberaceae; historical notes and a compilation of important recent papers appear in Burtt (1972). In a paper rich in information on older literature, Burtt & Smith (1972a) concentrated on 47 "key species" in an attack on the snarled early history of the family. Because so much has been written about the Zingiberaceae, the present historical discussion is limited to selected recent changes and major problems, the most controversial of which may be the choice of rank for the group often called subfam. Costoideae.

Subfamily Costoideae is commonly raised to the rank of family by modern authors, particularly those concerned with systems of classification and interrelationships of families on a broad scale (Cronquist; Dahlgren; Takhtajan; Thorne; and Tomlinson, 1962, 1969). In contrast, others who have worked intensively on the taxonomy within the groups under consideration have relegated Costoideae to the subfamilial rank (Burtt & Smith, 1983; Holttum, 1950; Maas, 1972 and subsequent updates), and Hutchinson gave it only tribal status.

That differences separating Costoideae from other Zingiberaceae span a wide spectrum of characters helps to counterbalance the fact that many of the differences are based on small samplings of species. Costoideae stand apart vegetatively in having strongly developed main stems, spirally arranged leaves, closed leaf sheaths (also true of some Zingiberoideae—see Spearing) bearing ligules of a characteristic nature (Tran van Nam), and no aromatic oil cells. The flowers have nectaries confined within cavities (vs. rising into the floral tube), may differ in anatomical details (Rao *et al.*), and lack apparent lateral staminodes, which is also true of some Alpinieae, and which is possibly due to fusion with the labellum. Embryologically, Costoideae may be distinguishable by the nature of the nucellus, by having a tetrasporic (vs. monosporic) megagametophyte (Mauritzon) and an expanded cotyledon (vs. being haustorial—see Weisse, 1932), and by additional characters. Pollen of Costoideae is usually panto- or diaperturate (vs. mostly inaperturate) and has thin to thick exines (cf. *Hedychium, Canna*—see Erdtman; Maas, 1972; Punt). The two groups are further separated by differences in anatomy (Tomlinson, 1956, 1962, 1969), flavonoids (Williams & Harborne), and centers of distribution. Most, but not all, chromosome numbers in Costoideae are multiples of nine, but the broadly ranging numbers in Zingiberoideae also include multiples of nine. Raghavan & Venkatasubban's assertion that chromosomal morphology is another distinction was not borne out by Sharma & Bhattacharyya.

Beyond the evident need for confirmatory surveys, reluctance of some authorities to elevate Costoideae to the rank of family may rest partly upon the emphasis given technical and vegetative characters versus that given the fundamentally "zingiberaceous" flower structure that links the two groups. Flower structure is traditionally a weighty character for delineating families of Zingiberales.

Schumann (1904 and earlier) broke subfam. Zingiberoideae into three tribes differing primarily in the number of locules in the ovary, the nature of the placenta, and the form of the lateral staminodes. Holttum (1950) transferred *Zingiber* from Schumann's Zingibereae (and consequently changed the name of this tribe to Alpinieae) to the Hedychieae, which should be renamed Zingibereae if this transfer is accepted. (Cytological support given by Mahanty for the transfer was dismissed as unsound by Burtt & Olatunji; better corroboration is provided by the plane of distichy of the leaves.) In 1972 Burtt & Olatunji placed *Zingiber* in a tribe of its own, thereby increasing the total of tribes to four: Alpinieae Meisner, Zingibereae (beware of disparate applications of this name), Hedychieae Duchartre, and Globbeae Meisner.[5] Dissatisfied with tribal delimitations, Burtt (1972; see also Burtt & Smith, 1972b; Smith, 1980a) discussed limitations on the taxonomic value of placentation and the nature of the lateral staminodes and agreed with Weisse (1933) that, although continued surveys are needed, the transverse plane of distichy on the aerial shoot in relation to the rhizome may distinguish Alpinieae from Hedychieae, in which the plane is parallel (as in Zingibereae *sensu* Burtt & Olatunji and those Globbeae examined by Weisse).

Zingiberopsis Hickey, a genus of three species of fossil leaves dating back to the Late Cretaceous and known from Alberta, North Dakota, Wyoming, and Colorado, was placed in the Zingiberaceae by Hickey & Peterson. Widespread in Eurasian sediments of Eocene to Pliocene age, zingiberaceous trilocular fruits and arillate seeds of *Spirematospermum Wetzleri* (Heer) Chandler resemble those of the modern Asian *Cenolophon oxymitrum* (K. Schum.) Holttum (Friedrich & Koch, 1970, 1972).

Chemical information on Zingiberaceae is scanty in relation to the size of the family. The summary that follows was condensed chiefly from surveys in Gibbs, Williams & Harborne, and Hegnauer. The aromatic oils of Zingiberoideae are rich in monoterpenoids (among them linalool, camphene, pinene, sabinene, borneol, camphor, cineole, and many others—the last three, according to Hegnauer, often the chief constituents of the oil). Sesquiterpenoids (including bisabolene, curcumenes, humulene, caryophyllene, zingiberene, turmerone, atlantones, zerumbone) are common and (hydrocarbons among them) sometimes predominate in the oil. Likewise widespread among aromatic plants, phenylpropane compounds are represented in zingiberaceous oils, sometimes as major components, by cinnamic acid and at least one derivative. Flavonoids are abundant, and Zingiberaceae (a small sample of Zingiberoideae) "form a chemically well defined group in which a variety of common (quercetin and kaempferol) and more unusual (myricetin, isorhamnetin and syringetin) flavonols occur in glycosidic combination with glucuronic acid, rhamnose or glucose" (Williams & Harborne, p. 226).

Mostly because of their aromatic oils, derivatives of Zingiberaceae have been used since ancient times as spices and condiments, in perfumes, and medicinally. Among the many products obtained from the family are ginger (prin-

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[5] Tribal names used here differ from those in Burtt (1972) in the spelling of Alpinieae and in the changed authorship of Hedychieae to reflect its valid publication by Duchartre (Dict. Hist. Nat. **13**: 356. 1849.)

cipally rhizomes of *Zingiber officinale* Roscoe); turmeric (rhizomes of *Curcuma longa* L. (*C. domestica* Valeton), an ingredient of curry powders and the source of a yellow dye used like the more expensive saffron); melegueta pepper (seeds of *Aframomum Melegueta* (Roscoe) K. Schum.); cardamom (capsules and seeds of *Elettaria cardamomum* (L.) Maton and substitutes from other species); and galangal (*Alpinia officinarum, A. Galanga* (L.) Willd.). An "arrowroot" starch is extracted from rhizomes of *Curcuma angustifolia* Roxb. and other species. Some of the many genera grown as ornamentals under warm conditions are *Alpinia, Hedychium, Kaempferia* L., *Nicolaia* Horan. (*Phaeomeria* Lindley ex K. Schum.), and *Roscoea* James Sm. Species from a number of genera have been used as sources of fibers or pulp. (Among several works dealing with economic aspects of Zingiberaceae are Burtt, 1977a, 1977b, 1980; Ilyas; Morton, 1981; Perry; Purseglove; Rosengarten; and Schumann.)

References:

Under ordinal references, see Costerus (1916b); Cronquist (1981); Czaja; Daghlian; Dahlgren; Davis; Erdtman; Gibbs; Hegnauer; Horaninow; Humphrey; Hutchinson; Lakela & Craighead; Mahanty; Mauritzon; Morton; Olatunji; Perry; Poppleton *et al.*, Potztal; Purseglove; A. S. Rao & Verma; V. S. Rao; V. S. Rao & Gupte; V. S. Rao, Karnik & Gupte; V. S. Rao & Pai; Rickett; Roscoe; Satô; Schachner; Sharma; Small; Takhtajan; Thorne; Tomlinson; Venkatasubban; Ward; Williams & Harborne; and Wunderlin.

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1. **Hedychium** J. G. Koenig in A. J. Retzius, Obs. Bot. **3:** 61 ("73"). 1783.

Upright, often large (*H. coronarium* to 3 m tall), [frequently epiphytic] herbs, the unbranched, leafy aerial stems borne on horizontal rhizomes and dying after flowering. Leaf blade inserted immediately above the sheathing base [or on a short petiole], usually attenuate at both ends, sometimes bearing soft, pale, matted hairs abaxially. Inflorescences usually spicate [rarely branched], with large, crowded, spirally arranged [or reportedly sometimes whorled], imbricate bracts covering the axes, each bract usually subtending multiple flowers [or the bracts divergent from the then exposed axis, enfolding 1 or more flowers]. Flower bracteolate, fragrant, white and often with yellow toward the base of the labellum and the bases of the lateral staminodes [or colored differently, the colors then usually yellows to reds or sometimes purple]. Calyx tube short, split along 1 side [or entire], 3-lobed to apparently 1-lobed, usually glabrous with indument concentrated at the apex (*H. coronarium*). Corolla tube long and slender, projecting beyond [or shorter than] the subtending bract, much longer than [or infrequently about as long as] the calyx. Lateral staminodes 2, broad, petaloid and showy; labellum, the broadest and showiest component of the flower, abruptly [or gradually] narrowed at base, usually apically cleft, the depth of apical notch, width, and overall shape highly variable, more or less obcordate in *H. coronarium* [to Y-shaped, wedge-shaped, or elliptic]; filament about as long as the labellum, sometimes slightly shorter [to much longer]; pollen grains spherical, inaperturate or uniaperturate (in *H. coronarium* the aperture, when present, ulceroid and not clear in surface view, *fide* Saad & Ibrahim). Ovary 3-locular, with many ovules per locule, glabrous to sericeous, the style filiform, lying in a groove in the corolla tube and filament, and protruding apically beyond the anther. Capsule loculicidal, 3-locular (fruiting specimens not seen from the United States). Seeds variably shaped, with initially red (becoming yellowish) arils, these lacerate on mature seeds. Base chromosome number mostly 17. TYPE SPECIES: *H. coronarium* J. G. Koenig.[6] (Name from Greek, *hedys*, sweet, and *chion*, snow.)

A genus of approximately 50 to 60 species, about a third of them described since Schumann's (1904) revision and many unclearly delimited, in two subgenera, HEDYCHIUM and EUOSMIANTHUS K. Schum.[7] The largely Himalayan center of distribution encompasses northeastern India, Bangladesh, the upper Ganges River, and Nepal. Continuing to the south and east with a diminished number of species, the probable natural range of *Hedychium*, outlined by southern China, Vietnam, the Philippines, Java, and Sulawesi, crosses Wallace's line but does not reach New Guinea or Australia. At the western extreme,

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[6] Burtt & Smith (1972a, p. 190) have argued against rejection of this and others of Koenig's specific names due to publication in a work in which Linnaean binomials were not consistently used.

[7] Wallich (1853) and Horaninow (1862) each recognized four subgroups of unspecified rank, two of which remain of interest: "*Gandasulium* Horan." and "*Macrostemium* Horan.," adopted by Baker (1892) at the rank of section and distinguished by the relative lengths of the stamen and labellum. Later, Schumann (1904), employing characters of the inflorescence and its bracts, divided the genus into "subgen. *Gandasulium* Horan." and subg. *Euosmianthus* K. Schum. Lourteig (1972) changed the name of the former to subg. *Hedychium*, since it includes the type species of the genus, and adopted for the latter "subgenus *Macrostemium* Horan. (sensu *Euosmianthus* Schum.)," with *H. Gardnerianum* Wallich ex Roscoe as lectotype. Although earlier than *Euosmianthus*, *Macrostemium* was published without designation of rank and thus, according to the ICBN, 1978, lacks nomenclatural priority at the rank of subgenus. It seems reasonable, nevertheless, to maintain *H. Gardnerianum* as lectotype for subg. *Euosmianthus* K. Schum.

Hedychium peregrinum N. E. Br. is endemic to Madagascar. The natural distribution of *H. coccineum* Buch.-Ham. ex James Sm. doubtfully includes Sri Lanka (Burtt & Smith, 1983). Species of this widely cultivated genus are scattered in other regions largely, if not completely, as a result of human activity. *Hedychium coronarium* grows extensively outside of cultivation in warm regions worldwide. Habitats of species of *Hedychium* range from tropical to temperate, at altitudes approaching 3000 m, in usually (but not always) open, typically wet places: often shores, moist slopes, and edges of forests. Several species are epiphytic or facultatively so.

Subgenus HEDYCHIUM (subg. *Gandasulium* (Horan.) K. Schum.) (inflorescence compact, usually broadly ellipsoid or ovate in outline, with wide, imbricate bracts covering the rachis) is represented in the southeastern United States by *H. coronarium*, ginger-lily, butterfly-lily, garland flower, which has escaped cultivation into various wet habitats in Florida (and according to Small, but not substantiated in recent checklists, in eastern Georgia and southeastern Louisiana). Although obscured by cultivation, the natural range of *H. coronarium* probably lies within the generic center of distribution described above. In that region *H. coronarium* is fertile (see, for example, Roxburgh, Mukherjee), although in some or all of the regions into which it has been introduced, production of fruit appears to be rare. Harling thought deficiency of pollinators to be a more likely explanation for low fertility of this species in Ecuador than incompatibility between members of the probably highly clonal population there. Self-incompatibility, however, has been reported in *Hedychium* (Holttum, 1950), and the plant illustrated in FIGURE 1 failed to set fruit with its own pollen. These reproductive limitations notwithstanding, *H. coronarium* can be an aggressive invader aided by strong rhizomatous growth and possibly distributed by fragmentation and flotation of rhizomes. It forms dense clumps or extensive colonies, in tropical America covering large areas and reportedly sometimes having a deceptively indigenous appearance (Beadle, Standley & Steyermark).

The name "*Hedychium coronarium*" is applied to various portions of a problematic complex that also involves the names *H. maximum* Roscoe, *H. flavum* Roxb. (non Roscoe), *H. flavescens*, *H. chrysoleucum* Hooker, *H. urophyllum* Lodd., *H. Elwesii* Baker, and *H. subditum* Turrill (*H. flavum* Roscoe). Baker treated most of these as varieties of *H. coronarium* separated from each other primarily by the coloration of the flowers. Emphasizing this character and the shape of the labellum, Schumann (1904) elevated most to specific rank, as did Turrill in a thorough, illustrated discussion of the matter. In Turrill's paper an expanded set of vegetative and reproductive characters augments the persistently important floral coloration. Studying living plants, Naik & Panigrahi uncovered intergradation in the colors of flowers among the species; they preferred using the structure of the inflorescence and the form of the labellum for taxonomic purposes and reassembled *H. coronarium* in its broader sense. Orchard, Lourteig, and Burtt & Smith (1983) have separated *H. flavescens* from *H. coronarium* at the specific level. If judged from the works cited above, *H. coronarium* sensu stricto is characterized by having the flower purely white or tinged with yellow or green, the calyx glabrous or nearly so and proportionately

FIGURE 1. **Hedychium.** a–n, *H. coronarium:* a, unbranched stem rising from horizontal rhizome, × $\frac{1}{12}$; b, portion of stem showing ligulate leaf bases, × ½; c, cross section of stem, × 6; d, detail of leaf showing venation, × 6; e, cross section of leaf sheath, × 6; f, inflorescence, × ½; g, flower, showing split, 1-lobed calyx, narrow petals with incurled margins, 2 broad lateral staminodes, labellum with bifid apex, and single sta-

short, the labellum about as wide as long, and the white staminal filament either about as long as or shorter than the labellum. The complex as a whole is recognized by having each bract with multiple mostly white to yellow flowers, each with a large labellum and usually broad lateral staminodes.

As a genus, hedychiums are robust rhizomatous herbs with unbranched aerial stems bearing terminal, usually spicate, many-flowered inflorescences. The fragrant flowers, usually a few per bract, tend to have lopsided calyces usually split along one side; each flower has a longish, narrowly cylindrical corolla tube with none (vs. one in *Odontychium* K. Schum.) of the lobes appendiculate; two strongly developed (vs. inconspicuous in *Alpinia*), petallike lateral staminodes; a protruding (vs. very short in *Brachychilum* (R. Br. ex Wall.) Petersen), usually bilobed, or emarginate labellum with an otherwise entire (vs. denticulate in *Odontychium*) margin; and a long, exserted stamen. As an example illustrating that "a number of genera [in Zingiberoideae] may be distinguished by their leaf flavonoid profiles," Williams & Harborne (p. 224) pointed out that myricetin glycosides are the predominant flavonoids in *Hedychium* (9 species studied).

Smith (1980a) found the new genus *Stadiochilus* R. M. Sm. to resemble *Hedychium* in having the corolla tube grooved to accommodate the style (known also in *Brachychilum* and *Zingiber*), in the form of the corolla lobes, and in having a long filament. Smith (p. 14) stated that "if a pair of petaloid lateral staminodes were added to *Stadiochilus* we should have a perfectly good *Hedychium* rendered slightly anomalous by the upright, rather pendulous labellum."

Most chromosome counts in *Hedychium* have yielded the somatic number 34, although the genus appears to be prone to polyploidy and aneuploidy, with numbers varying even within species (see especially Mukherjee). The following somatic numbers have been reported in species of *Hedychium*: 18 (*H. coronarium*, see Hsu), 24 (reported once in *H. thyrsiforme* Ham., but contradicted by further study—see Mahanty), 26, 36, 50, 51, 52, 54, 66, and 68. Most of these numbers up to 66 have been reported in *H. coronarium* sensu lato, as well as in other species. Raghavan & Venkatasubban observed general similarity in the size and morphology of chromosomes among the six(?) species of *Hedychium* that they studied. Similarly, although the chromosomal morphology was not identical in any two taxa, Sharma & Bhattacharyya noted "a gross resemblance" among 10 species and varieties of *Hedychium*. Those two authors, in good agreement with Mukherjee, found the chromosomes of *He-*

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men, × ½; h, adaxial side of anther (note thin style passing between the 2 locules, the stigma protruding apically), × 3; i, abaxial view of anther, × 3; j, lateral view of stigma, × 15; k, adaxial view of stigma, × 15; l, diagrammatic cross section of corolla tube above calyx, the lumen in black, the style in groove above lumen unshaded, × 6; m, diagrammatic cross section of flower slightly above ovary, showing calyx (outer unshaded layer not adnate to corolla tube), corolla tube (unshaded), 2 epigynous nectar glands, and style (in groove in corolla tube), × 6; n, diagrammatic cross section of ovary, showing locules and axile placentae, × 6.

dychium generally to be short, varying gradually in length within each complement. The different potential species of *Hedychium* studied by Sharma & Bhattacharyya had chromosomes with the primary constrictions nearly submedian to median and varied in the numbers of pairs bearing secondary constrictions. Mukherjee and Sharma & Bhattacharyya reported meiosis in *H. coronarium* to be mostly normal or nearly so; Mukherjee recorded 96 percent pollen fertility in material from northeastern India. According to Holttum (1950), hybrids are easily produced in *Hedychium*.

The three main layers of the walls of pollen grains in *Hedychium* resemble those of the more thoroughly studied *Canna* and certain other genera. In *Hedychium coronarium* a grainy, thin, acetolysis-resistant, presumably exinous layer overlies a thick, acetolysis-degradable, almost certainly intinous layer with a radially patterned infrastructure. The third, innermost layer is hygroscopic and lacks a radial pattern (Erdtman & Praglowski). Although generalizations would be premature and substantial variations have turned up, there are indications that pollen roughly as described above may be widespread among Zingiberales (see Saad & Ibrahim; Erdtman, 1963; Hesse & Waha, under *Canna*; Kress *et al.*; Kress & Stone, under *Canna*).

Meager data point to sphingids as the predominant pollinators of *Hedychium coronarium* and probably most other species of the genus. Pollen may sometimes be transferred on the wings of butterflies (Müller).

Accessory embryos were observed to arise from synergids but not to develop beyond early stages in *H. acuminatum* Roscoe (Sachar & Arora).

Hedychium coronarium, H. coccineum, H. Gardnerianum Roscoe, *H. spicatum* Buch.-Ham. ex James Sm. (see Winters & Corbett) and several other species are cultivated, mostly under warm conditions. The fragrant, showy flowers of *H. coronarium* are valued for making Hawaiian leis (see Neal). Volatile oils from flowers and rhizomes of this and possibly other species are useful in perfumery. Rhizomes of *H. spicatum*, sometimes sold as the drug "kapur(a) kachari" and sometimes in a fragrant powder, abir, lend their scent to tobacco, incense, soaps, face powders, hair oils, and fabrics, and they are thought to repel insects. Medicinal uses of derivatives of *H. spicatum* and other hedychiums are available in Chaturvedi & Sharma, Cooke, Dixit & Varma, Perry, Pineda-Ocampo *et al.*, Sastri, B. D. Sharma (1974, 1975), and the papers by S. C. Sharma *et al. Hedychium coronarium* has attracted attention as a rapidly growing source of pulp for paper. This rhizomatous species sometimes becomes a weedy pest in places where sugar cane is grown (Beadle).

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CANNACEAE A. L. Jussieu, Gen. Pl. 62. 1789, "Cannae," nom. cons.

(CANNA FAMILY)

Large, usually rhizomatous herbs with unbranched aerial stems. Leaves large, with open, eligulate sheaths. Flower asymmetric, with a staminodial lip (labellum) and a variable number of additional petallike staminodes [or none], 1 fertile, partly petaloid stamen, and 1 more or less flattened, colorful style rising from a 3-locular ovary with septal nectaries. TYPE GENUS: *Canna* L.

1. **Canna** Linnaeus, Sp. Pl. **1:** 1. 1753; Gen. Pl. ed. 5. 1. 1754.

Plants often 1 to several meters tall, often glaucous, mostly glabrous (sometimes with an ephemeral, woolly indument on leaves and stem [or inflorescences]). Rhizomes branching sympodially, sometimes thickened, these and aerial stems with mucilage canals or cavities. Leaves with the blades often asymmetric, the sheath clasping the stem to the insertion of the blade or partly free; stomata predominantly paracytic. Inflorescences terminal on leafy shoots, spicate or branched, each branch with a 2-keeled prophyll. Flowers showy, in homodromous cincinni of 2 flowers (1 flower of the pair typically not developing, rarely with 3 flowers), each flower or pair subtended by a bract and sometimes with scalelike bracteoles, erect [to pendulous], colors mostly yellows and reds. Sepals 3, free, persistent, lanceolate to elliptic. Petals 3, usually unequal, usually basally connate and adnate to the androecium and style to form a tube, upright or reflexed, deciduous. One stamen fertile and partly petaloid, enfolding the style in the bud, with a marginal anther, this sometimes appearing superficially to be 2-locular (but generally interpreted as a 1-locular half-anther); the other androecial members sterile, one of these curled [or straight] forming the labellum, the remaining 3 or 2 [or none in subg. *Distemon*] mostly large, erect, broadened, and petallike (flowers rarely with a fifth sterile staminode); pollen deposited onto the side of the style in the bud, the pollen grains mostly spherical, usually with small spinules, inaperturate (sometimes with 1 or 2 pores *fide* Nair, 1962). Ovary covered with conspicuous, sap-bearing protuberances, each of the 3 locules with numerous anatropous ovules on an

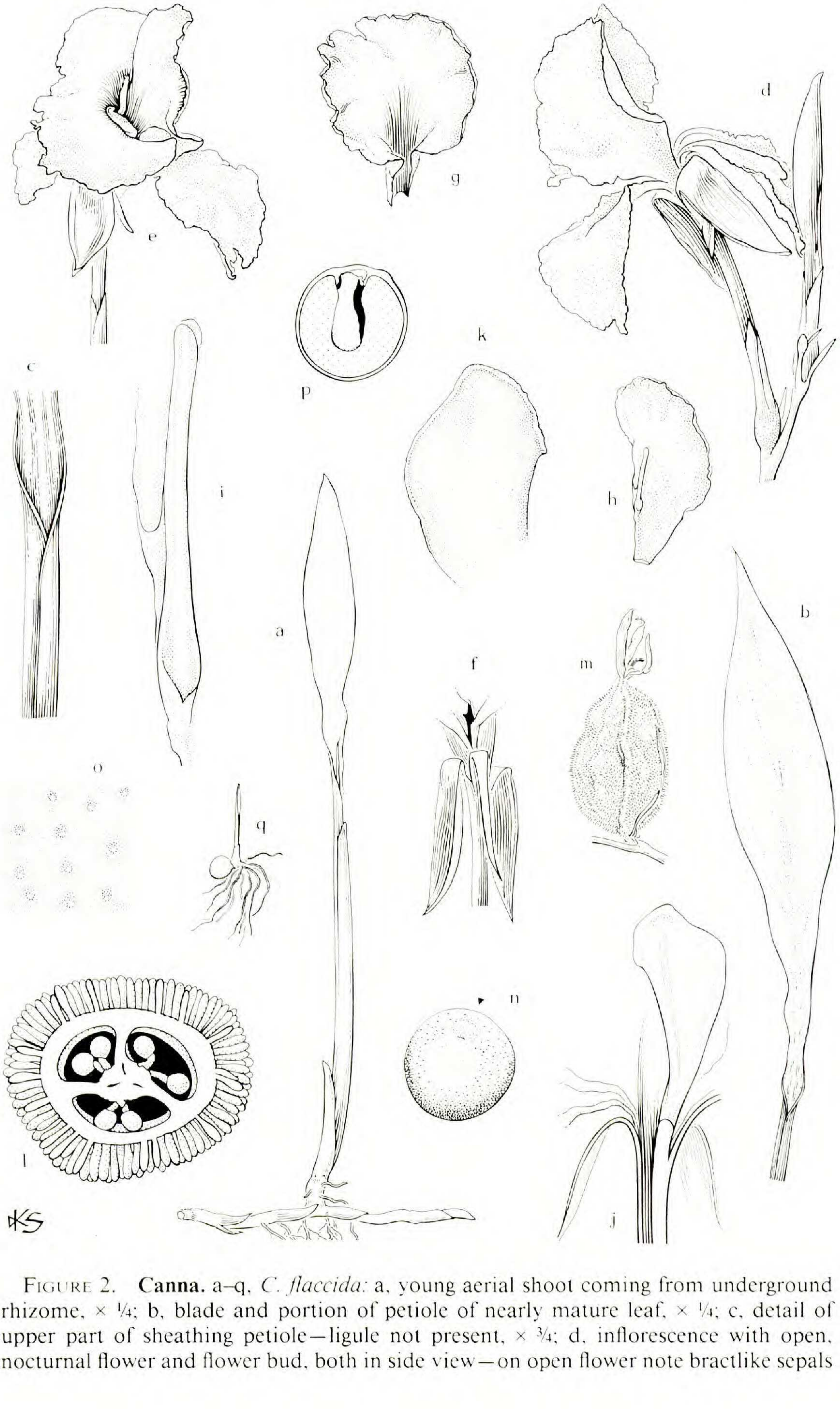

FIGURE 2. **Canna.** a–q, *C. flaccida:* a, young aerial shoot coming from underground rhizome, × 1/4; b, blade and portion of petiole of nearly mature leaf, × 1/4; c, detail of upper part of sheathing petiole—ligule not present, × 3/4; d, inflorescence with open, nocturnal flower and flower bud, both in side view—on open flower note bractlike sepals

axile placenta; style opposite the fertile stamen; stigmatic surface terminal and decurrent along an edge of the style. Capsule globose to oblong-ellipsoid, tuberculate-bristly, loculicidally dehiscent or the seeds released by breakdown of the pericarp. Seed globose or nearly so, dark colored, hard, opening by a slit, with an arillike tangle of hairs arising from the funiculus, these hairs remaining in the fruit; with abundant nutritive tissue ("chalazosperm") derived from the chalazal region; endosperm initially nuclear, reduced to a thin layer in the mature seed. Embryo linear, straight, extending into a cavity at the end of the seed. Radicle and plumule developing apart from the remnant of the seed, connected to it by a cotyledonary appendage. Megagametophyte (embryo sac) essentially of the Polygonum type. Base chromosome number 9. LECTOTYPE SPECIES: *C. indica* L.; see N. L. Britton, Fl. Bermuda, 86. 1918. (Name from Greek *kanna,* cane.)

A distinctive monogeneric family with a problem-free circumscription, in contrast with its internal taxonomic and nomenclatural disarray. The usually quoted estimate of about 50 species in *Canna* was approximately halved in the revision by Segeren & Maas, and according to Jiménez (citing personal communication), Maas has since compressed his estimate to only seven species. The genus is centered in the American tropics and subtropics, including the West Indies; species occupying scattered warm areas in the Old World were probably introduced by humans, although agreement on this point is not unanimous.

Cannas are characterized by an asymmetric, showy flower with a staminodial labellum, two or three large, relatively unspecialized, petaloid, sterile staminodes (in ours), and one partially petaloid fertile stamen. The inferior ovary and capsule are tuberculate, the capsule containing several dark-colored, hard, nearly spherical seeds with stomata on the seed coats and a tangle of emergences on the funiculus. The leaves lack ligules and pulvini. Mucilage canals pass through the rhizomes and unbranched aerial stems.

The four genera of Cannaceae recognized by Horaninow were reduced to sections and subgenera of *Canna* by Petersen (1888) and Baker (1893), respectively. In the only revision of the entire genus written during the twentieth century, Kränzlin retained subg. DISTEMON (Bouché) Baker and, subsuming

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at base, reflexed petals, and 5 dissimilar, petaloid staminodes (labellum to lower left, 2 small sterile staminodes to upper right under the letter "d"), × ½; e, frontal view of open flower, labellum to lower right, fertile half-anther and tip of stigma visible in center of flower, × ½; f, detail of flower to show reflexed petals, × ½; g, expanded staminode, × ½; h, fertile stamen with half-anther attached to left margin, × ½; i, detail of half-anther after dehiscence, × 3; j, vertical section near center of flower to show petals, staminodes, and style adnate to floral tube, × 1; k, tip of style showing stigmatic line around apex, × 2; l, diagrammatic cross section of inferior trilocular ovary, 3 septal nectaries visible as black slits near center, the wall finely tuberculate, the ovules anatropous, axile, × 5; m, mature capsule crowned by persistent sepals, × ½; n, mature seed, × 3; o, detail of seed coat showing finely pitted surface (with stomata—not visible), × 25; p, seed in diagrammatic section (cut along line indicated by arrow in "n"), "chalazosperm" evenly stippled, × 3; q, seedling still attached to seed, × ½.

Baker's other subgenera in subg. (Eu-)CANNA, divided the latter into sects. BIALATAE and TRIALATAE. Section TRIALATAE (which should be called sect. CANNA) comprised four subsections. Winkler's infrageneric classification was essentially the same, except that the subsections were designated series. In a revision of the species in northern South America, Segeren & Maas thought it "very doubtful" that sections BIALATAE and TRIALATAE should be maintained and did not keep them in their formal treatment, which is the course accepted in the present paper.

Subgenus CANNA (staminodes two or three, in addition to the labellum; labellum reflexed) is represented in the southeastern United States chiefly by *Canna flaccida* Salisb., $2n = 18$, which is probably the only indigenous species. Sometimes called "golden canna," "yellow canna," or "bandana of the everglades," it occurs on the Coastal Plain from South Carolina to Texas, and in the West Indies, Central America, and northwestern South America. Flowers of this striking species have reflexed petals and very showy, broad, soft, yellow staminodes with undulate margins; the bases of the leaves are gradually tapered. A similar species with a wide range in warm regions south of the United States, *C. glauca* L., $2n = 18$, has been reported from Louisiana and Texas (see Thieret; *Godfrey & Tryon 274* [GH] from South Carolina is probably also referable to this species). *Canna glauca* (*C. angustifolia* L., *C. stricta* Bouché, both synonyms from Segeren & Maas) differs from *C. flaccida* most saliently in its erect petals and narrower staminodes. (Whether or not the staminodes of *C. glauca* are mottled is a point of disagreement.) *Canna indica*, indian-shot (with an ample synonymy), $2n = 18, 27$ (also probably 36; plus other dubious numbers reported), has escaped cultivation sporadically in the Southeast, as well as in much of tropical Asia, Africa, and elsewhere. This species was cultivated in Europe as early as the sixteenth century. Its capsules and predominantly red flowers marked with (or sometimes entirely?) yellow are smaller than those of the preceding species (e.g., the widths and lengths of the staminodes are about 1–1.5 × 4–6 cm vs. 1.5–2 × 8–10 cm in *C. glauca* and 8–9 × 9–11 cm in *C. flaccida*; measurements from Segeren & Maas). *Canna indica* sometimes produces fertile hybrids with *C. glauca* despite some meiotic irregularities and diminished fertility. *Canna edulis* Ker-Gawl., $2n = 18, 27$, often cultivated for its edible rhizome, appears in Ward's checklist of plants native or naturalized in Florida and as a synonym of *C. indica* in Segeren & Maas.

Described by Kränzlin as "ein uferloses Meer," the cultivated cannas are an assortment of probably over 1000 horticultural varieties. Most of these fall into two main groups, both of which persist following cultivation or escape in the Southeast: *Canna* × *generalis* Bailey does so sporadically in several states, and *C.* × *orchiodes* Bailey was reported as growing apart from cultivation in North Carolina by Crutchfield. Flowers of these two diverse, intergrading hybrid lines are large (reaching 20 cm in diameter in *C.* × *orchiodes*) and display a rich array of colors, mostly reddish and yellowish hues, sometimes pastels or white, with the staminodes often spotted, streaked, and bordered. Foliage and stems are bronzed in some. Because *C. flaccida* is a genetically influential ancestor of *C.* × *orchiodes*, confusion between these two is especially likely. *Canna flaccida* has a longer floral tube (over 5 cm vs. ca. 2.5–5 cm in *C.* ×

orchiodes and less than ca. 1.5 cm in *C.* × *generalis*) and a longer capsule (4–6 cm vs. shorter and sterile in *C.* × *orchiodes*). Both *C.* × *orchiodes* and *C. flaccida* differ from *C.* × *generalis* and the other species in having petals reflexed or becoming so and flowers that are generally more delicate and flowing. (For further comparison of the large-flowered cannas, see Bailey, 1923; Crutchfield; and Mukherjee & Khoshoo, 1970d.)

Much literature on *Canna* revolves around elucidating the ancestry and cytology of *C.* × *generalis* and *C.* × *orchiodes* and morphological changes that have taken place in the course of their development since the mid-1800's. The history of the cultivars is clouded by loose application of names in early records. From the multifaceted investigations along these lines by Mukherjee and Khoshoo, *Canna glauca, C. indica, C. iridiflora* Ruiz & Pavon, and *C. Warszewiczii* A. Dietr. stand out as the most likely principal progenitors of the multiple lineages known as *C.* × *generalis*. Selected additional (but not entirely congruous) references useful in this connection are Anonymous (1898), Bailey (1923), and Donahue.

Like their four supposed ancestors, most cultivars of *Canna* × *generalis* are diploids with normal or nearly normal meiosis. A small proportion are meiotically irregular interchange heterozygotes; others are sterile triploids that tend to form trivalents at metaphase I.

During the 1890's, plants of *Canna* × *generalis*, in this case "Crozy cannas," were crossed with *C. flaccida* to yield *C.* × *orchiodes*. That the genome of *C. flaccida* is strongly differentiated from those of the putative ancestors of *C.* × *generalis* is suggested by the complete sterility of *C.* × *orchiodes*, which has highly irregular meiosis in its diploid cultivars and forms few, loose trivalents in the triploids. On the other hand, Kränzlin mentioned fertile hybrids between *C. flaccida* and *C. Warszewiczii*. (The accuracy of this report depends upon the accuracy of Kränzlin's opinion that a plant breeder misapplied the name *C. "nepalensis"* to *C. flaccida*.) Baker (1894) described *C. flaccida* × *iridiflora* as the origin of (fertile?) fine garden forms.

If one considers the genetic intercompatibility among (and not limited to) the probable ancestors of *Canna* × *generalis*, confusion in defining species of *Canna* is hardly surprising. A related confounding factor is that cannas have long been transported about the world by humans (undoubtedly with operation of the founder principle, release of segregating hybrid progeny into new habitats, vegetative propagation of new forms, and artificial selection). The pantropical complex centered around *C. indica* is a troublesome example, involving several possible species. A second puzzling example is *C. flaccida*, which differs only slightly from *C. Reevesii* described by Lindley from specimens grown from seeds sent to him from China.

A further source of taxonomic confusion in *Canna* is a likely overemphasis of certain characters. For instance, in a series of papers, Honing analyzed the genetics of the coloration of flowers and vegetative parts in *C. glauca, C. indica,* and other possible species. In 1939 (VI) he explicitly rejected Kränzlin's classification, concluded that the most obvious differences distinguishing *C. indica* and certain other "bialatae" depend on only a few Mendelian factors, and proposed placing five names (including *C. indica*, excluding *C. glauca*) in synonymy. (Honing's studies were summarized by Khoshoo & Mukherjee (1970b), who suggested that members of nearly the same collection of species, including both *C. glauca* and *C. indica,* may be differentiated at an ecospecific level.) Red color in the flowers is a monogenic dominant trait influenced in expression by at least 22 other genes and linked to a set with recessive lethal alleles. The presence of two vs. three staminodes in addition to the labellum has repeatedly emerged (e.g., Baker, 1894; Costerus, 1916a; Jiménez; Kirchoff, 1983b; Segeren & Maas) as a character of questionable taxonomic value, varying within a species and even on a single plant, yet this character alone distinguishes Kränzlin's sections "Bialatae" and "Trialatae."

Species of *Canna* are predominantly diploids with $2n = 18$. Triploidy (which appears to have arisen repeatedly in artificially selected cultivars) and infrequent tetraploidy have been detected only in species for which diploid counts are also reported. (Compilations of chromosome numbers are available in Segeren & Maas; Mahanty; Khoshoo & Mukherjee, 1970a; Sharma; and Satô). Satô described and illustrated chromosomal morphology for *Canna edulis, C. indica,* and *C. glauca,* all $2n = 18$, which differ from each other in distributions of lengths of chromosomes, positions of centromeres, and locations of satellites and secondary constrictions. Mahanty concluded from a study of six species that species of *Canna* form a very homogeneous group.

As in Marantaceae, the pollen in Cannaceae is deposited on the style while in the bud, either directly onto or near the stigma. It is widely assumed, although hardly tested, that self-fertilization plays an important role in the breeding system. Mukherjee & Khoshoo (1970b) (see also Darwin) found the few "elemental" species that they studied, cultivated outside of their natural ranges, to be predominantly autogamous, whereas displacement of the anther and stigma necessitated a shift to outbreeding in the cultivated hybrids. (Garden cannas are usually propagated vegetatively.)

The fragrant flowers of *Canna flaccida* open about dusk for a single night throughout the year in South Florida. Swamps, marshes, shores, and pine savannas are the habitats of this species; in the United States *C. glauca* and *C. indica* likewise occupy wet places. This is at least sometimes true of hybrid cultivars growing outside of cultivation.

In much of the American tropics and subtropics, including the southeastern United States, *Canna* is larval host to a skipper butterfly, *Calpodes ethlius* (Cramer), which at times is severely destructive to the plants (see Clark & Clark, Cockerell, Evans, Young) and which is a pest on the related *Maranta arundinacea* grown commercially in the West Indies (Purseglove). The larvae, which build tentlike structures protected by rolled or folded leaves, are parasitized by possibly two genera of wasps.

As determined for *Canna* × *generalis* and *C. indica,* the thick wall of the pollen grain has three main layers. Much reduced, the exine, which takes the form of scattered spinules and may also extend around the grain as a thin skin (Hesse & Waha), rests on a thick, bilayered intine. The outer intinous layer, the "exintine" (Kress & Stone), is honeycombed with radial channels and overlies the unchanneled "endintine." Comparable in structure to germinal pores of more typical pollen grains, the "omniaperturate" grains of *Canna* appear to have their entire surface suitable for hydration, other interactions with the stigma, and emergence of the pollen tube. The channels in the intine possibly function as reservoirs of compounds connected with incompatibility mechanisms or otherwise with germination of the pollen (Hesse & Waha). For details on the structure of the pollen, see Kress & Stone, Rowley & Skvarla (1974, 1975), Scheer & Franke, Skvarla & Kelly, and Skvarla & Rowley. (Also see discussion of *Hedychium* in the present paper.)

Useful not only as ornamentals, some species of *Canna* have starchy rhizomes, for which especially *C. edulis* is used as a source of food for livestock and humans. Possibly first domesticated in northern South America (Gade), this species is cultivated in warm regions around the world, sometimes on a commercial scale. The product from Australia is called "Queensland arrowroot." A current project of the New York Botanical Garden Institute of Economic Botany is the development of a clone of *Canna* with the largest starch grains known from any plant. The hard, more or less spherical, dark-colored seeds have been employed in sundry easily imaginable ways from ammunition to rosary beads, and they have also been used as an ingredient in a substitute for coffee. One example sufficiently underlines their renowned durability: a seed about 600 years old taken from within a rattle recovered from an Argentinian tomb grew into a flowering individual of *Canna compacta* Roscoe (Lerman & Cigliano). Burning the plants is said to produce an insecticidal smoke. Extracts from *C. indica* and other species have molluscicidal activity of interest in the control of schistosomes (Mahran *et al.*). Additional uses of cannas, especially extensive medicinal applications, are listed in Hegnauer, Kränzlin, Morton (1981), and Perry.

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MARANTACEAE Petersen in Engler & Prantl, Nat. Pflanzenfam. II. **6:** 33. 1888, nom. cons.

(ARROWROOT FAMILY)

Erect [or scrambling or climbing] small to large herbs of diverse habit. Rhizomes branching sympodially, usually with short internodes. Plants glabrous or with usually unicellular hairs, each surrounded at the base by a cluster of inflated epidermal cells. Branches variably developed, sometimes clustered at or above the ground, often widely divergent, each branch bearing (in the following order) a basal, 2-keeled prophyll above a short internode, usually a bladeless sheath (interphyll) above a second short internode, a series of petiolate leaves, and a terminal inflorescence often overtopped by axillary growth [inflorescences sometimes arising directly from the rhizome]. Leaves typically distichous, basal or cauline, with open, often auriculate [rarely ligulate] sheaths, and often asymmetric [often variegated] blades, those of leaves on a shoot either homotropous (i.e., the broader halves all on the same side—right or left—of the midrib) [or antitropous, the broader halves on alternating sides]; petiole with a usually pubescent pulvinus at the insertion of the blade; stomata mostly paracytic. Inflorescences highly variable, [completely or] partly tightly condensed to diffusely branched, bracteate; bracts frequently large and colorful, mostly sheathing. Flowers asymmetric, usually in mirror-image pairs, each pair or group of pairs subtended by a bract and a basal prophyll, [with or] without bracteoles. Sepals free. Petals usually unequal and usually connate basally and adnate to the androecium and gynoecium to form a tube. Outer androecial cycle represented by [0 or] 1 or 2 antesepalous, petallike staminodes; the 3 members of the inner cycle all different: the "cucullate staminode"[8] forming a

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[8] A disorderly profusion of names has been applied to the 2 inner sterile staminodes, both of which are hoodlike. Those adopted in the present paper are translated from extensive use in German and have been used in English by other authors. The cucullate staminode (FIGURE 3, g) is also known as the hooded staminode, Kappenblatt, Kapuzenblatt, or style-holding staminode. The callose staminode (FIGURE 3, h) has also been called the callosed or callused staminode, Schwielenblatt, and labellum. Particularly misleading, the last term is used for structures in Cannaceae and Zingiberaceae that are uniquely homologous within each family.

sterile pouch concave toward the axis of the flower and enclosing the style, with 1 or 2 appendages inserted on the edge away from the fertile stamen and arching over the concavity; the "callose staminode" bent into a hood, concave toward the axis of the flower (facing the concave side of the cucullate staminode), usually with a thickening protruding inward from the face of the side nearer the fertile stamen [or with a second thickening on the other side]; the fertile stamen usually borne on the side of the flower adjacent to the other flower of the pair, with a unilocular half-anther inserted laterally on [and sometimes adnate to] a petaloid appendage [this sometimes short and inconspicuous]. Gynoecium with 1 [or 3] locules developing and [0 or] 1 anacampylotropous fertile ovule per developing locule, this nearly basal on an axile placenta; nectaries septal; style curled inward upon release from the cucullate staminode, with a specialized pad basal to the stigma for deposition of pollen in the bud; stigma in a depression between 3 variably developed flaps. Fruit indehiscent or dehiscent into 3 valves, dry [or fleshy]. Seeds variable in shape, basally arillate [or not, especially in indehiscent fruits], hard, operculate; endosperm formation nuclear, endosperm much reduced or lacking in mature seed, perisperm abundant and penetrated by a curved or straight (sometimes basally forked) canal originating as a vascularized chalazal intrusion into the progressively curving nucellus; embryo U-shaped. Megagametophyte (embryo sac) fundamentally of the Polygonum type, antipodal cells sometimes undergoing secondary divisions. Chromosome numbers highly variable, the base numbers including 4, 6, 9, 11–13. TYPE GENUS: *Maranta* L.

A sharply defined family of 25 to 30 genera and probably more than 400 species (usually sorted into two tribes) typical of understory vegetation in wet regions pantropically, but sometimes reaching subtropical or infrequently warm-temperate areas. The greatest concentration of species is in the South American tropics, with lesser centers of distribution in tropical West Africa and tropical Asia. Especially widespread, the genus *Thalia* L. occurs throughout much of Africa, where it may or may not be indigenous, and from southern South America to the southeastern United States. (The family is also represented in Florida by *Maranta arundinacea*, an infrequent escape from cultivation.) Outstanding among the genera, which only exceptionally contain more than 20 species, *Calathea* G. F. W. Meyer probably encompasses considerably more than 130. This genus and *Thymocarpus* Nicolson, Steyerm., & Sivadasan are the only representatives of the tribe Phrynieae Petersen (ovary with three fertile locules and usually three fertile ovules) in the New World. The tribe Maranteae (ovary with one fertile locule and ovule) is restricted to the New World, except for *Thalia*, as mentioned above.

Marantaceae are unified as a family by their open, usually eligulate leaf sheaths and a pulvinus (or "callus") at the insertion of the blade. Tomlinson (1961) pointed out that the strongly developed aerial branching system sets the family apart from other Zingiberales (but the presence of a prophyll followed by one or more incomplete leaves is insufficient to distinguish Marantaceae).

The asymmetric flowers, usually borne in homodromous pairs, have a unique explosive pollination mechanism (described below), one or two showy outer staminodes, two hoodlike inner staminodes positioned face to face (one with one or two lateral appendages, the other usually with a thickening protruding from the surface), a half-anther connected to a petaloid appendage (also true of Cannaceae), and a uni- or trilocular ovary with one nearly basal ovule per locule. The abundant nutritive tissue in the usually arillate seed is penetrated by one or two canals. The embryo is curved.

While there has been little contention about the delimitation of the Marantaceae as a family, the definition and nomenclature of taxa within it have a troubled history. Although fundamental to the studies that followed, Koernicke's monographs (1859, 1862) bear little resemblance in detail to relatively recent treatments. Eichler provided detailed morphological analyses essential for comparing plants as complex as Marantaceae and a firm foundation for his taxonomic treatments of the genera in the New World. These contain very little emphasis on individual species, however. Eichler died while working on the Marantaceae for the *Flora Brasiliensis*, for which the account of this family was completed by Petersen, who also authored the brief and conservative treatment of the family in the first edition of the *Natürlichen Pflanzenfamilien*. Major generic reorganizations, especially among the taxa of the Old World, appeared in Schumann's treatment, which is the most recent revision of the family as a whole. Schumann recognized 26 genera, over twice the number in any of the other works mentioned above. Loesener updated Schumann's revision with a few alterations. In an effort to alleviate persistent confusion in the delimitation of genera, Andersson (1981a) reevaluated the neotropical genera using a wide array of characters and (some taxonomic changes notwithstanding) felt that his studies largely confirmed the validity of Schumann's genera.

Andersson's (1977, 1981a) proposed view of the early evolution of Marantaceae departs markedly from the emphases on a single character and on geographic distributions of the traditional tribal division. According to Andersson, the family probably originated in Africa (see Holttum for a contrary view); the five informal groups into which he sorted the New World genera hypothetically reflect distinct phyletic lines, each with its closest relatives in the Old World. Tomlinson (1961) failed to distinguish the traditional tribes anatomically, Williams & Harborne found them not to differ in distribution of flavonoid constituents, and Bisson *et al.* could find no cytological support for their maintenance.

Marantaceous inflorescences vary from congested capituliform or spicate arrangements to those with clustered subunits or infrequently individual flowers separated by elongated internodes. Spathelike, often colorful bracts are frequently arranged in imbricate spirals or distichous rows, or in some species they are widely separated. Growth pattern ranges between strongly monopodial and more or less sympodial. Branching may reach several orders of complexity (with repeated patterns or not) or may be nearly completely suppressed. As is evident from two analyses of the architecture of inflorescences in Marantaceae (Eichler; Andersson, 1976), a fundamental uniformity underlies the confusing diversity.

Andersson's attempt to unify the terminology applied to the inflorescence is useful if it is borne in mind that the subunits that he recognized are not all constantly discernible throughout the family and that his naming of different levels within the inflorescence deemphasizes repetition in pattern. Like a vegetative branch, an axis in a marantaceous inflorescence begins with two short internodes, the first bearing a two-keeled prophyll (three-keeled in some flower pairs) and the other bearing an (often-suppressed) interphyll. As the result of repeated condensed basal branching, clusters of branches often falsely appear (e.g., in *Thalia dealbata*) to be axillary to a single bract. Monopodial axes bearing bracts typically subtending flower pairs or clusters of flower pairs were termed "florescences" by Andersson. The pairs of flowers are borne either singly or in often much-condensed sympodial arrangements ("florescence components"). Because the morphological nature of the flower pairs remains unsettled, they cannot be counted among taxonomic links to the Cannaceae, which also sometimes have paired flowers. Positions of associated foliar structures, symmetry and time of opening of the flowers, and supposed occasional manifestations of the missing terminal flower have been cited as evidence that the flowers of a pair in the Marantaceae are the two lateral members of an ancestrally three-flowered dichasium (see F. Müller, Eichler). Alternatively, the positions of the bracteoles in some specimens indicate one flower as lateral and the other as terminal (see Andersson, 1976). Kirchoff (1983b) concluded that in Marantaceae the members of a pair originate simply by division of an apical meristem.

Arils on seeds of Marantaceae appear to promote dispersal in at least three ways. Schumann (see also Humphrey) noted a correlation between dehiscent fruits and arillate seeds in the family and also stated that expansion of the aril can force apart the valves of such fruits. Eichler observed that the aril jutting from a partially dehisced fruit can help free it from the enclosing bracts. Bright coloration and deposits of lipids, which are at least sometimes present in marantaceous arils, point to a third role for these structures: the attraction of birds (Ridley) and ants. In a study of species of *Calathea* and several genera of ants, Horvitz & Beattie found that these insects sometimes (with variation between species) transport the seed by using the aril as a handle. The ants take the seed into their nest (perhaps a favorable, protected microsite for germination), use the aril as food (thus promoting germination), and bury the remainder of the seed in a refuse heap near the nest, where the effectively planted seed lies in a bed enriched by decaying organic waste and may be protected by the ants.

Prior to the tripping of the pollination mechanism, the style, confined by the cucullate staminode, develops tension, and the half-anther deposits pollen onto a specialized region below the stigma (FIGURE 3, k-13). One or two appendages rise from one margin of the cucullate staminode and arch across its concave side, thereby also extending over the style (FIGURE 3, g). As might be guessed from the appearance of these "triggers" (and as has been confirmed for some species), their displacement by a suitable bee releases the springlike style from its confinement. When thus tripped, the style bends suddenly inward toward the callose staminode, which apparently functions in bracing the precisely arranged mechanism, in orienting the insect visitor, and as as anvil for the stroke of the style. The inward-moving stigma scrapes pollen from the insect, which is then at least sometimes smeared with sticky fluid from a glandular region on the style, followed by a dusting with pollen from the pad just behind. According to Kennedy, at least three genera of Marantaceae deposit the pollen on the proboscidial fossa, out of reach of the bee when cleaning itself. After pollination, the curled style and (when present) an appendage beyond the stigma (FIGURE 3, j-16) block further loss of nectar and/or autogamy. Euglossine bees, among which are pollinators of many orchids, are the principal pollinators of Marantaceae in the New World (Kennedy) but do not range into the southeastern United States (Michener). (Supplementary references on pollination are Andersson, 1981a; Eichler; Gris, 1859; Hildebrand; Knuth; H. Müller; Purseglove; and Schumann.)

The function of the peculiar chalazal canals in the seeds appears to be connected with the vascular tissue that defines their course early in development. Because the canals are closed off in the mature seed, they are unlikely to be conduits for air or water (Grootjen). Diverse inclusions of chalazal tissue in seeds of Zingiberaceae, Cannaceae, and Musaceae neither resemble nor initiate such canals.

Species of *Calathea*, especially *C. Allouia* (Aublet) Lindley, serve as minor sources of starch. Derivation of starch from *Maranta arundinacea* is discussed under that genus. The leaves of species of *Calathea* yield a wax of high quality (see Ayensu *et al.*). Several genera, among them *Maranta*, *Calathea* (e.g., *C. zebrina* (Sims) Lindley, zebra plant), *Ctenanthe* Eichler, and *Stromanthe* Sonder, are cultivated for their decorative foliage.

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1. **Thalia** Linnaeus, Sp. Pl. **2:** 1193. 1753; Gen. Pl. ed. 5. 3. 1754.

Usually tall (1–4 m in the southeastern United States), erect, large-leaved herbs of wet habitats. Glabrous or with soft hairs on axes of the inflorescence, bracts, floral parts, fruits, and leaves. Foliage leaves mostly or entirely basal, petiolate, homotropous. Inflorescences variably and usually richly branched, often with 3 or more axes falsely appearing to arise from a single node, the main axis clearly monopodial (*T. dealbata*), or forming pseudodichotomies with axillary branches (*T. geniculata*), the lateral branches with further bifurcations or not, the penultimate units conspicuous kinked or zigzag axes ("florescences" or "rachises") bearing a pair of flowers at each kink. Flowers of

FIGURE 3. **Thalia.** a–m, *T. geniculata:* a, portion of inflorescence, many flowers fallen, other flower buds enclosed within bracts (spathe and prophyll), cf. FIGURE 4, d, × ½; b, pair of tripped flowers (mirror images) enclosed within bracts (1 and 2), the continuing axis of inflorescence branch (unshaded circle) removed just above base of bracts, the

each pair laterally appressed and enclosed in a pair of unequal bracts, the smaller bract adjacent to the rachis (this bract the prophyll on the condensed shoot bearing the flower pair), the condensed shoot subtended by the larger, abaxial, boat-shaped bract (spathe), the spathes of several pairs often imbricate along the rachis while immature, spathes and prophylls both falling off with the fruits, leaving the rachis naked; other foliar organs in the inflorescence caducous or persistent. Corolla and androecium purplish or blue, sometimes pink [or white]. Sepals very small, distinct, hyaline. Corolla lobes distinct or nearly so, nearly equal to unequal, variably fused at the base with the androecium. Outer staminode constricted basally, showy and protruding, borne nearly abaxially to the rachis; cucullate staminode with 2 appendages, markedly connate with the callose staminode, this a very broad, bilobed hood provided at the edge adjacent to the fertile stamen (with which it is sometimes strongly connate) with an oblique, inward-jutting thickening; fertile stamen with its half-anther inserted laterally on a variably developed petaloid lobe. Gynoecium unilocular by abortion, with 1 fertile ovule; style twisted when triggered, free from the androecium, with an appendage derived from the initially adaxial rim of the stigmatic cleft projecting back into the flower after pollination. Fruit ellipsoid to subglobose, indehiscent, with a thin pericarp. Seed single, subglobose or ellipsoid, sometimes slightly flattened, with a smallish aril, the perisperm penetrated by 2 curved canals originating from a basal bifurcation and flanking the embryo. TYPE SPECIES: *T. geniculata* L. (Name commemorating Johann Thal, ca. 1542–1583(?), German physician and naturalist, who died after falling from a carriage.)

A cohesive, predominantly South American genus of seven or a few more species ranging from the southern United States, where two species are indigenous, to the West Indies, Argentina, and Uruguay, and represented throughout much of tropical (especially western) Africa by the often-mentioned "*Thalia Welwitschii* Ridley" and two other possible species (see Hepper, Koechlin, Gagnepain). As discussed below, it is likely that the widespread African populations resulted from human activity.

Said to be the largest-leaved herb native to the southeastern United States,

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floral parts numbered (see below for key to numbers), × 5; c, right-hand flower from "b," × 5; d–k, parts of flower from "c," × 3; l, diagrammatic cross section of ovary, oriented as in flower (c), the fertile ovule above with its micropyle toward the center septal nectary, the 3 septal nectaries and 2 empty, compressed locules below, × 12; m, fertile, basal ovule, the micropyle to lower left, × 12.

Key to floral parts in "b"–"k": 1, outer, lower bract (spathe) enclosing pair of flowers; 2, upper, inner bract (prophyll) enclosing pair of flowers; 3, upper, adaxial petal; 4, lateral petal (second lateral petal not visible); 5, outer staminode; 6–10, stamens of inner whorl—6, cucullate staminode (encloses style until pollination mechanism is triggered); 7, petaloid lobe, which together with callused lobe, 8, forms callose staminode, this connate with 9, fertile half-stamen, and 10, sterile half-stamen (the callose staminode connate at the other margin with 6); 11, lateral sepal; 12, inferior ovary; 13, pollen-bearing area of style (in "b" with pollen); 14, stigmatic cavity after pollination (note pollen); 15, style; 16, stylar appendage.

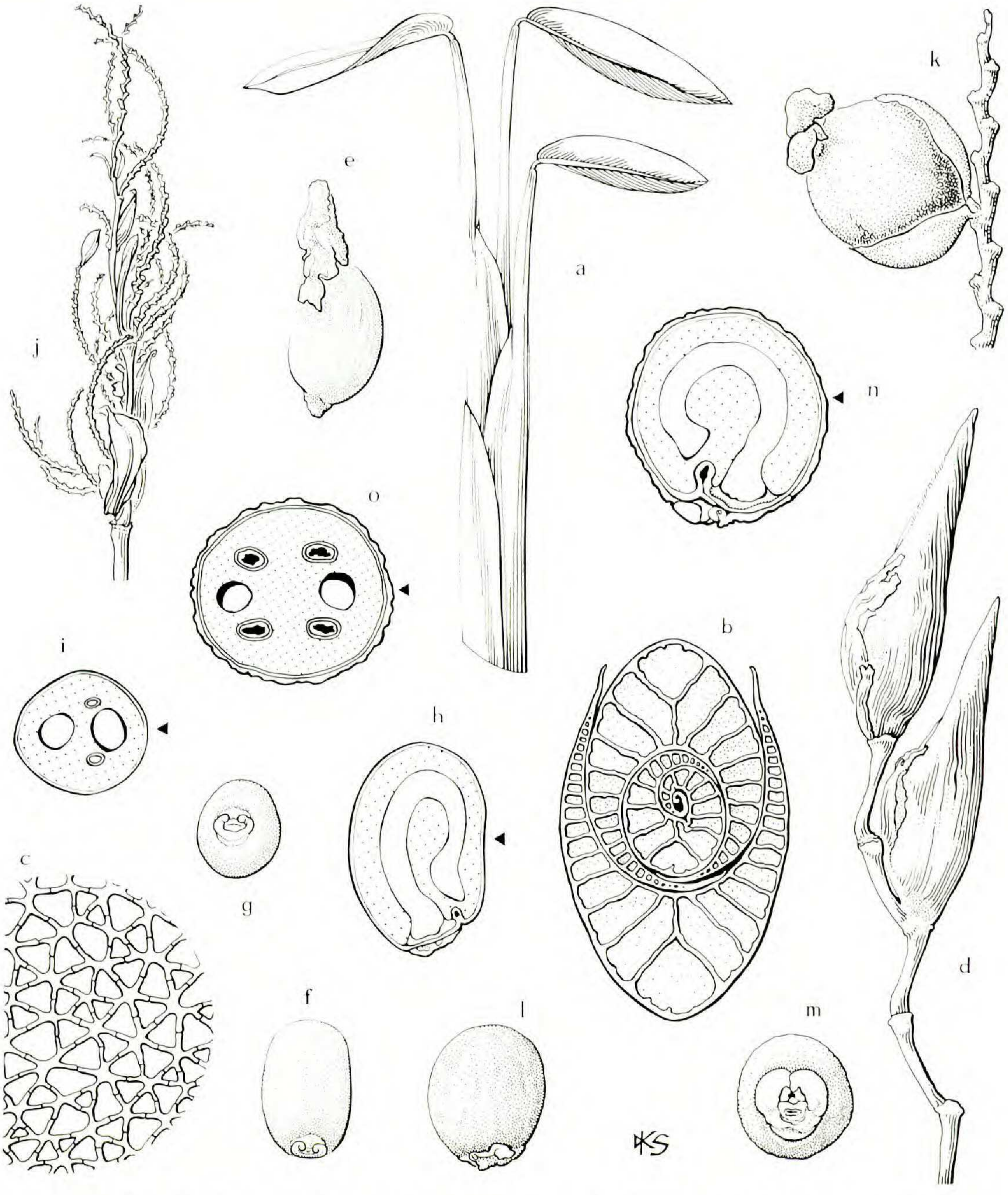

FIGURE 4. **Thalia.** a–i, *T. geniculata:* a, young leafy shoot (small)—note bladeless sheathing leaf at base, overlapping sheaths, and pulvinus between blade and petiole, × ¼; b, diagrammatic cross section of sheaths of 2 leaves and of a third, much younger leaf to show vertical plates of tissue (vascular bundles omitted) plus horizontal diaphragms (stippled), × 1¼; c, detail of a diaphragm from "b" to show connecting stellate cells with openings between, × 25; d, tip of inflorescence branch with 2 mature fruits, each enclosed by pointed outer and frayed inner bracts (spathe and prophyll, respectively), × 2; e, mature fruit with marcescent floral parts on top, × 2; f, seed, removed from fruit—note aril at base, × 2; g, base of seed to show aril, × 2; h, diagrammatic vertical section of seed (through arrow in "i"), thick part of aril to left at base, invagination of chalaza in black, perisperm stippled, curved embryo unshaded, outer seed coat heavy black line, inner seed coat unshaded, × 3; i, cross section of seed (oriented as in "h") at level of arrow in "h," showing seed coats, perisperm, embryo, and chalazal canals in perisperm, × 3. j–o, *T. dealbata:* j, inflorescence axes after fruits have fallen to show

Thalia geniculata L. (*T. divaricata* Chapman, *T. trichocalyx* Gagnep., *T. Welwitschii*) in this country is restricted to Florida but extends southward from Mexico and the West Indies approximately to Buenos Aires, Argentina. It is essentially absent from the drainages of the Amazon and upper Orinoco rivers. A distribution map of this species broadly defined with superposed highly variable but poorly correlated characters is provided in Andersson's revision of the "*Thalia geniculata* complex." The main problem tackled in this study was a taxonomic evaluation of the three African species of *Thalia*, the morphological divergence of which Andersson attributed to a "bottle neck effect" following supposed introduction of *T. geniculata* into Africa, possibly in the ballast of ships sailing from the Greater Antilles during the slave trade. As a consequence of this hypothetically recent and artificial separation, all African thalias were synonymized with *T. geniculata*. Andersson mentioned that plants fitting the original description of the tropical American *T. trichocalyx* grow in Florida, but he also included this species under *T. geniculata*. *Thalia geniculata* f. *rheumoides* Shuey, with red coloration on the leaves, inflorescences, and particularly the petioles, occurs in east-central Florida. Miège's report of $2n = 18$ for *T. geniculata* is based on material from Senegal; the provenance of the specimen used by Mahanty for a photograph of the chromosomes ($2n = 26$) is not specified.

Thalia dealbata Fraser ex Roscoe[9] (*T. barbata* Small), powdery thalia, $2n = 12$, grows on the Coastal Plain from South Carolina to Texas, in Oklahoma, Arkansas, and Missouri. This species differs most saliently from *T. geniculata* in having more compact, more rigid inflorescences with a less dichotomous aspect (internodes on the rachis 2–3 mm vs. 5–16 mm); smaller flowers and bracts (the spathe of each pair mostly less than 1.5 cm long vs. mostly longer); and the pruinose bloom for which it is named.

Delimitation of *Thalia*, which has no obviously close relatives, has been less troublesome than that of other genera of Marantaceae. Thalias are usually large herbs of wet places; they have homotropous leaves and paniclelike inflorescences with distinctive zigzag axes. The purplish flowers (ours) are borne in tight, bract-enclosed pairs without bracteoles; each has one conspicuous outer staminode, a very short corolla tube, minute sepals, a cucullate staminode with

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[9] I have not seen an illustration of this species said by Roscoe to have been published by Fraser in Ic. Bot. Gard. Liverpool, probably in 1794.

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branching pattern—compare with "d" and with FIGURE 3, a, × ½; k, tip of inflorescence axis with a single fruit enclosed at base by prophyll and subtending spathe and tipped by marcescent floral parts, × 2; l, side view of seed, showing basal aril, × 2; m, base of seed to show aril, × 2; n, vertical section of seed (at level marked by arrow in "o"), showing thick part of aril to left, outer seed coat wavy, inner seed coat unshaded, basal invagination of chalaza in black, perisperm stippled, embryo unshaded (note that the 2 chalazal canals in perisperm branch from the invagination shown here), × 3; o, cross section of seed (at level marked in "n"), showing curved embryo (unshaded) in perisperm with parallel chalazal canals (much longer than in "i" and thus each cut twice) in black, × 3.

two (vs. usually one in other Marantaceae) appendages, a style with a large backwardly pointing appendage, and a unilocular ovary. The seed has a usually small aril and two (vs. usually one) curved chalazal canals. Andersson (1981a), confirmed the taxonomic isolation of *Thalia* and compared it with his "Myrosma group" of genera, *Halopegia* K. Schum., and *Hypselodelphys* (K. Schum.) Milne-Redhead, from all of which *Thalia* is distinguishable by the characterization above.

In the principal revision of *Thalia*, Schumann named four subgenera, which were retained by Loesener: Euthalia (containing our *T. dealbata*), Arthrothalia (containing only *T. geniculata*), Sarothalia, and Anomothalia. In view of the small size of the genus (and because the first two subgeneric names contravene the ICBN, 1978) their continued recognition is of questionable value.

The two species of *Thalia* in the Southeast grow in or bordering ponds, streams, swamps, ditches, hammocks, and other wet places. Both flower from spring through autumn. Andersson (1981b), on the basis of observations in the field, thought plants of *T. geniculata* to be self compatible and geitonogamous. In the Southeast various insects reportedly visit flowers of *Thalia*; however, only carpenter bees (*Xylocopa*) are known to trigger the pollination mechanism (D. Austin, see acknowledgments). A gas-filled space between the seed and pericarp in *T. dealbata*, the canals in the perisperm, and the persistent waxy bracts may promote dispersal by water (see Grootjen).

Seeds of *Thalia* "*divaricata*" (*geniculata*) are reportedly eaten by ducks in Florida (McAtee). The inner portion of the boiled rootstock of *T. geniculata* is said to be suitable as food for humans (Morton, 1977). *Thalia dealbata* is sometimes cultivated in aquatic gardens.

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2. **Maranta** Linnaeus, Sp. Pl. **1:** 2. 1753; Gen. Pl. ed. 5. 2. 1754.

Perennial, or perhaps sometimes annual, erect [or prostrate] herbs of diverse habit, [some species without aerial stems or branched only basally,] when branched aerially the main shoot and axillary growth often divaricate-pseudodichotomous, usually terminating in inflorescences. Rhizome fleshy, with scale-covered stolons (*M. arundinacea*). [Glabrous or] with pale indument of variable length, texture, and density on stems, leaves, and ovary (*M. arundinacea*). Leaves homotropous [except in *M. Ruiziana* Koern.], separated by distinct internodes, variegated in some species, basal and cauline [or entirely basal], extremely diverse in shape (lanceolate to elliptic with the apex acuminate in *M. arundinacea*), the sheath sometimes extending to the pulvinus, this usually with an adaxial tuft of hairs. Inflorescences racemiform to diffusely branched, with the axillary and main shoots divergent (in the uncrowded inflorescences of *M. arundinacea* and some other species, the pattern of growth neither clearly monopodial nor clearly sympodial) [some species with compact, spicate branches ("florescences"), these actinomorphic or bisymmetrical]; flower pairs borne singly or in few-membered clusters ("florescence components"), each pair with a prophyll but no apparent interphyll, and no [or rudimentary] bracteoles, the pedicels of the 2 flowers and their common stalk of variable lengths, 1 flower apparently terminal and on a longer pedicel, the other apparently lateral and on a shorter pedicel; bracts sheathing, persistent or caducous. Flowers white [to bluish, purplish, or otherwise]. Sepals free, equal, acute, fibrous. Corolla with a usually long tube, this usually gibbous at the base and bent and adnate to the androecium and style; corolla lobes subequal, cucullate at the apex. Outer staminodes 2 (or 3), unequal, conspicuous and flaglike (obovate and usually emarginate in *M. arundinacea*); cucullate staminode with 1 lateral appendage; callose staminode often 2-lobed; fertile stamen with the petaloid half basally connate with and apically wrapped around the cucullate staminode (*M. arundinacea*); pollen grains inaperturate or possibly sometimes uniaperturate. Ovary 1-locular by abortion with 1 fertile ovule; stigma in a usually funnel-shaped hollow formed by a pair of lips at the end of the style. Fruit indehiscent or sometimes 3-valved, ellipsoid, 3-angled in transverse aspect, with 1 seed (some cultivars of *M. arundinacea* seedless). Seed rectangular in longitudinal view, triangular in transverse view, with a pale yellow aril; perisperm canal straight, bifurcate apically. TYPE SPECIES: *M. arundinacea* L. (the only species included by Linnaeus in the *Species Plantarum*). (Named for the botanist Bartolommeo Maranta, died ca. 1560, a native of Venosa, Italy.)

About 20 species, many of them poorly defined, in four questionable subgenera, indigenous to tropical America, especially Brazil, with *Maranta Friedrichsthaliana* Koern. endemic to Costa Rica and *M. arundinacea* and *M. divaricata* Roscoe (= *M. arundinacea*?) also in Central America. No species is clearly native to the West Indies (see Howard for comments on three species collected in the Lesser Antilles). Since *M. arundinacea* has escaped cultivation and become naturalized sporadically in warm portions of both the Old and New Worlds, its original distribution can only tentatively and vaguely be stated as tropical South America and possibly Central America. Whether or not this species preceded Europeans in the West Indies is uncertain; it was clearly under cultivation there in the 1600's (cf. Hodge & Taylor, Purseglove, Sturtevant). Cultivated at least as far north as northern Florida, *M. arundinacea* has evidently become a minor element in the flora of South Florida. Small (p. 361) described it as occurring on "hammocks and moist soil, S. pen. Fla.," and in a few more recent publications (Ward; Morton, 1977), this species is accepted as growing without cultivation in Florida. However, its meager representation in other checklists and consulted sources should be noted. This representative of subg. MARANTA (divaricately branched; bracts few, not imbricated, convolute around the axis; flower pairs on long pedicels) has uncrowded, highly branched growth, leaves with long-attenuate apices, white flowers with the ovaries glabrous or pubescent on the corners, and thickened stolons.

In 1859 and 1862 Koernicke envisioned *Maranta* as a broadly circumscribed genus made up of four "Untergattungen" or (in his second paper) sections: EUMARANTA, STROMANTHE (Sonder) Koern., SARANTHE Regel & Koern., and XOROLEPIS Koern. Eichler retained part of Koernicke's sect. EUMARANTA as the genus *Maranta* and sorted the remainder of the former genus, with changes in the groupings, chiefly into the genera *Stromanthe* Sonder, *Saranthe* (Regel & Koern.) Eichler, and *Ctenanthe* Eichler, all of which have been maintained as genera with further adjustments in delimitation in subsequent revisions. Using characters concerned with the form and arrangement of bracts, coloration of leaves, habit, and structure of the inflorescence, Schumann named four new subgenera under *Maranta*: AUTOMARANTA (i.e., MARANTA), KOERNICKEA, CALATHEASTRUM, and FRIEDRICHSTHALIA.

Andersson (1981a), who rejected Schumann's subgenera, placed *Maranta* alongside *Monophyllanthe* K. Schum. to form his informal "*Maranta* group" and indicated that the two genera perhaps ought to be merged. Species of the

Maranta group tend to have long floral tubes; fibrous, acute sepals; the cucullate staminode with only one appendage; a funnel-shaped stigmatic orifice; flower pairs with elongate axes and without interphylls and (usually) bracteoles; an apically bifurcate perisperm canal in the solitary, mature seed; and usually homotropous leaves. *Maranta* differs from *Monophyllanthe*, according to Andersson, in having two equally developed outer staminodes (vs. one staminode reduced or absent) and in details of habit. Andersson concluded that the closest affinities of the *Maranta* group are with the African genus *Marantochloa* Brongn. & Gris, which differs in having three fertile ovules, instead of only one.

Saranthe, *Ctenanthe*, and *Stromanthe*, placed in the "*Myrosma* group" by Andersson, are evidently not strongly differentiated either from each other or from the *Maranta* group. With exceptions, these genera differ from *Maranta* in having proportionately shorter floral tubes, usually shorter internodes and more frequent bracteoles in the flower pairs, and a tendency to have the bracts on branches of the inflorescence (florescences) in a monosymmetric arrangement (vs. radially or bilaterally symmetrical). *Ctenanthe* and *Stromanthe* differ further from most species of *Maranta* in having antitropous leaves.

Any generalization about cytology in *Maranta* is hampered by reports on dubiously identified specimens, even at the generic level, and by substantial cytological heterogeneity. Vouchered survey work is needed. From the information we have, it appears that somatic chromosome numbers range between 18 and 52. (A diploid number of 8 was reported for *M.* "*nitida-picta*"—see Venkatasubban.) As judged from very limited data, cytological differences between species of *Maranta* extend to the lengths of chromosomes and the positions of centromeres. In *M. arundinacea*, $2n = 18$ (46, 48, 52 also reported), Satô encountered two long pairs of chromosomes with submedian centromeres, a medium-long pair with median centromeres, five short pairs (one with submedian centromeres, the remaining four with subterminal), and one very short pair with terminal centromeres.

According to one account in the collection of correspondence concerning *Maranta arundinacea* (Anonymous, 1893), the name "arrowroot" may have originated from the Carib *ara-ruta*, "mealy root"; alternatively, the name may stem from use of the rhizome in treating wounds from poisoned arrows. "Arrowroot" has become generalized to other plants with starch-yielding rhizomes, such as *Canna edulis*.

Produced in tropical countries worldwide, chiefly on the West Indian island of St. Vincent, true arrowroot starch is extracted from the tough, fibrous rhizomes of *Maranta arundinacea*. Easily digestible, the starch is particularly valuable for feeding infants and persons with special dietetic requirements. Additionally, it is or has been used like other starches, such as for starching laundry, in glue, and in the preparation of powders for the skin. Among the many medicinal uses are application internally and externally to counteract poisons and in poultices to treat various dermatological afflictions. Species of *Maranta*—among them *M. bicolor* Ker-Gawl. and the prayer plants, *M. leuconeura* Morren (including var. *erythroneura* Bunting)—are popular in homes and greenhouses for their decorative, sometimes variegated foliage. At least one cultivar of *M. arundinacea* has variegated leaves. (Additional references concerned with uses for *Maranta* are Ayensu, Hamilton, Hodge & Taylor, Morton (1977), Neal, Purseglove, and Sturtevant.)

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ADDENDUM

After this paper was completed, a specimen of *Thalia geniculata* cultivated indoors at the Arnold Arboretum flowered for the first time, allowing us to make the following observations.

In bud, the anther deposits large (ca. 100 μm in diameter when fresh) pollen grains onto the style within the cucullate staminode. Possibly functioning as a trigger, the stylar appendage in the open untripped flower rises as a steep uphill floor at the entrance of the floral tube. The pollination mechanism is extremely sensitive and is easily sprung by various minor disturbances. After being (artificially) triggered, the style twists and comes to rest blocking the floral tube, with the pollen-bearing portion against the outside of a pouch formed by a membrane extending between the callose staminode and the thickened lobe on it. Presence of numerous pollen grains in the stigmatic cleft suggests that self-pollination can occur in the absence of a pollinator during the stroke of the style. Consistent with this possibility, artificially triggered flowers readily formed fruit when bagged in bud or immediately following triggering. (It was impossible to bag flowers singly.) I have not ruled out the presence of pollen in the stigmatic cleft prior to release of the style, other forms of autogamy, or apomixis.